

Taxonomy of the Family Neilonellidae (Bivalvia, Protobranchia): Miocene and Plio-Pleistocene Species of *Pseudoneilonella* Laghi, 1986 from Italy

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Abstract. *Pseudoneilonella* Laghi, 1986 is considered a valid genus in the family Neilonellidae Schileyko, 1989. It is morphologically similar to *Neilonella* Dall, 1881, but with an external opisthodetic, instead of amphidetic, ligament. In both genera, a small, internal ligament is also present, mainly in the early growth stages. *Austrotindaria* Fleming, 1948 is also considered a valid neilonellid genus. It has an opisthodetic ligament and differs markedly from *Pseudoneilonella* and *Neilonella* by its delicate, poorly sculptured shell. Three bathyal species of *Pseudoneilonella* are known from the Mediterranean Plio-Pleistocene: *Pseudoneilonella pusio* (Philippi, 1844), *P. salicensis* (Seguenza, 1877) and *P. tenella* La Perna, sp. nov. A possible fourth species, *Pseudoneilonella* sp., was present in the Early Pliocene. Another species, *Pseudoneilonella taurinensis* La Perna, sp. nov. is described from the Middle Miocene of the Turin hills. In the European area (paleo-Mediterranean and Paratethys), *Pseudoneilonella* occurs since at least the Middle Miocene. *Pseudoneilonella latior* (Jeffreys, 1876) is a modern representative from the North Atlantic.

INTRODUCTION

The family Neilonellidae Schileyko, 1989 (= Saturniidae Allen & Hannah, 1986, non Boisduval, 1837), of recent institution, includes many species formerly assigned to the Malletiidae H. & A. Adams, 1858. Some taxonomic studies have been devoted to the Neilonellidae (Maxwell, 1988a; Warén, 1989; Allen & Sanders, 1996; Coan et al., 2000), but this family remains poorly known and without a full agreement about the genera belonging to it (Allen & Hannah, 1986; Maxwell, 1988a; Coan et al., 2000; Allen & Sanders, 1996). Like most protobranchs, neilonellids are mainly distributed in deep waters.

Two neilonellid species were formerly known from the Plio-Pleistocene of Italy, but recent studies shed new light on the composition and stratigraphic distribution of this group. The present paper is a contribution to neilonellid taxonomy, through the study of the fossil species from Italy and focusing on three genera: *Neilonella* Dall, 1881, *Austrotindaria* Fleming, 1948 and *Pseudoneilonella* Laghi, 1986.

MATERIALS AND METHODS

The Plio-Pleistocene bathyal deposits cropping out in Southern Italy (Figure 1) are rich in protobranch bivalves and other typically deep-sea taxa (Di Geronimo & La Perna, 1997; Di Geronimo et al., 1997; La Perna, 2003). The inferred paleodepths range from the slope break to some 1,000 m. The study material is mostly from author's collection, but voucher specimens are deposited in a public institution (MZB). Other

study material is from Middle Pliocene bathyal deposits of Rio Gambellaro, Romagna, Northern Italy (Tabanelli, 1993; Tabanelli & Segurini, 1995), and from the Middle Miocene of the Turin hills (Bellardi & Sacco collection).

The following abbreviations are used: IGNS = Institute of Geological & Nuclear Sciences, National Paleontology collection, Lower Hutt, New Zealand; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge; MRSN = Museo Regionale di Scienze Naturali, Turin; MZB = Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna; MZHU = Museum für Naturkunde der Humboldt-Universität, Berlin; coll. = collection; v(s) = loose valve(s); sh(s) = complete shell(s); L = shell length; H = shell height.

SYSTEMATICS

Class Bivalvia Linné, 1758

Subclass Protobranchia Pelseneer, 1889

Order Nuculoida Dall, 1889

Family Neilonellidae Schileyko, 1989

Genus *Pseudoneilonella* Laghi, 1986

Pseudoneilonella was erected by Laghi (1986) as a replacement name for *Saturnia* Seguenza, 1877, non Schrank, 1802, for those species similar to *Neilonella* Dall, 1881 but with an opisthodetic ligament. *Saturnia* and *Pseudoneilonella* are thus objective synonyms with the same type species (ICNZ, art. 67.8), i.e., *Nucula*

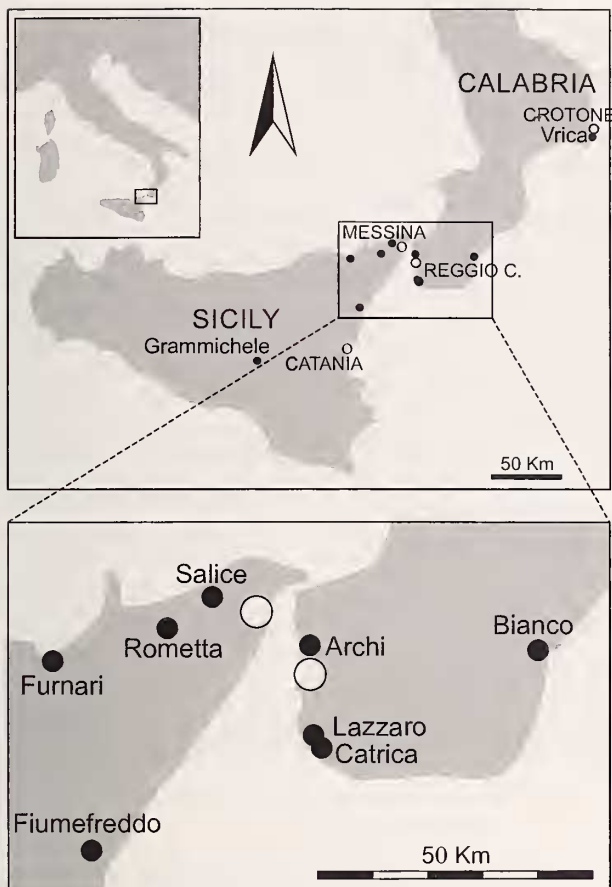


Figure 1. Collecting localities in Southern Italy (solid dots) and references: Vrica, Pliocene/Pleistocene boundary stratotype (Pasini, Colalongo, 1994); Bianco, Early Pleistocene (Di Geronimo, La Perna, 1997); Lazzaro and Catrica, Early-Middle Pleistocene (Di Geronimo, La Perna, 1997); Archi, Early-Middle Pleistocene (Di Geronimo et al., 1997); Salice, Early-Middle Pleistocene (Di Stefano, Lentini, 1995); Rometta, Middle Pliocene (Violanti, 1989); Furnari, Early Pleistocene (Di Geronimo, La Perna, 1997); Fiumefreddo, Early-Middle Pleistocene (Girone et al., 2006); Grammichele (Valle Palione), Early Pleistocene (Girone et al., 2006).

pusio Philippi, 1844 by monotypy (Seguenza, 1877b), in spite of the proposal of *Leda* (*Saturnia*) *pusio* var. *salicensis* Seguenza, 1877 as type species of *Pseudoneilonella* by Laghi (1986). It should be noted that Laghi's opinion of var. *salicensis* Seguenza, 1877 was biased by the misinterpretation of *Nucula pusio* Philippi, 1844 as *Ledella messanensis* (Jeffreys, 1870) (Di Geronimo & La Perna, 1997; La Perna, 2003). In other words, Laghi (1986) did not know the true *Pseudoneilonella salicensis* and applied this name to *Pseudoneilonella pusio*. As summarised by Di Geronimo & La Perna (1997) and La Perna (2003), var. *salicensis* Seguenza is involved in a long history of misidentification (Jeffreys, 1879; Locard, 1889; Laghi, 1986; Warén, 1989; Allen &

Sanders, 1996), which led this name to be applied to a Northeast Atlantic species, *Leda pusio* var. *latior* Jeffreys, 1876, improperly known as *Neilonella striolata* (Brugnonc, 1876) (Warén, 1989; Salas, 1996) or *Neilonella salicensis* (Seguenza, 1877) (Allen & Sanders, 1996).

Dell (1956) and Maxwell (1988a, b) remarked on the differences in the ligament characters of *Neilonella* and *Austrotindaria* Fleming, 1948. *Neilonella corpulenta* (Dall, 1881) (Recent, Caribbean), type species of *Neilonella*, has an external, amphidetic ligament (Figures 2a–e; see also Laghi, 1986: fig. 1c, pl. 9, figs. 1–3; Allen & Sanders, 1996: fig. 11), whereas it is opisthodetic in *Austrotindaria wrighti* Fleming, 1948 (Recent, New South Wales), type species of *Austrotindaria* (Figures 3a–f). Mainly based on this difference, Di Geronimo & La Perna (1997) and La Perna (2003) assigned two species from the Mediterranean Plio-Pleistocene to *Austrotindaria* instead of *Neilonella*, i.e., *Austrotindaria pusio* (Philippi, 1844) and *A. salicensis* (Seguenza, 1877), and considered *Pseudoneilonella* a junior synonym of *Austrotindaria*.

The occurrence in *Austrotindaria* of an edentulous gap in the hinge plate, dividing the tooth series into a posterior and an anterior row, has also been noted in the literature (Fleming, 1948; Dell, 1956; Maxwell, 1988a, b; Beu & Maxwell, 1990). Actually, a short “edentulous gap” occurs in *A. wrighti* (Figures 3c, d), but it consists of a small, elongate ligament pit (not clearly seen from the standard valve orientation), rather than of a smooth portion of hinge plate. This character in no way conflicts with the interpretation of *Austrotindaria* as a neilonellid, since the external ligament of this family develops through an early inner stage (Figures 7b, d, f) and a relict ligament pit can be preserved in the later growth stages, as an internal or external (above hinge) small pit (Figures 2d, e, 7h, i). The development of a short, poorly defined edentulous gap in *Pseudoneilonella* (Figures 7h, k) is probably related to these ontogenetic changes. This character was well described by Verrill & Bush (1898: 877–878) on *Neilonella corpulenta*: “Resilium very minute or nearly abortive, occupying a slight notch in the dorsal margin under the beak, external to the series of teeth, which are interrupted only by a small, thin edentulous space”. It is worth noting that a distinct, apparently functional inner ligament pit is present in the adult stages of small sized species (Figures 6b, g, 8i), suggesting heterochronic relationships between larger and smaller species. The neilonellid inner ligament is thought to be evidence of the affinities between this family and the Malletiidae, which also possess an early inner ligament, migrating outwards with growth (Okelmann & Warén, 1998).

Austrotindaria and *Neilonella* differ from each other profoundly in shell characters and the most obvious

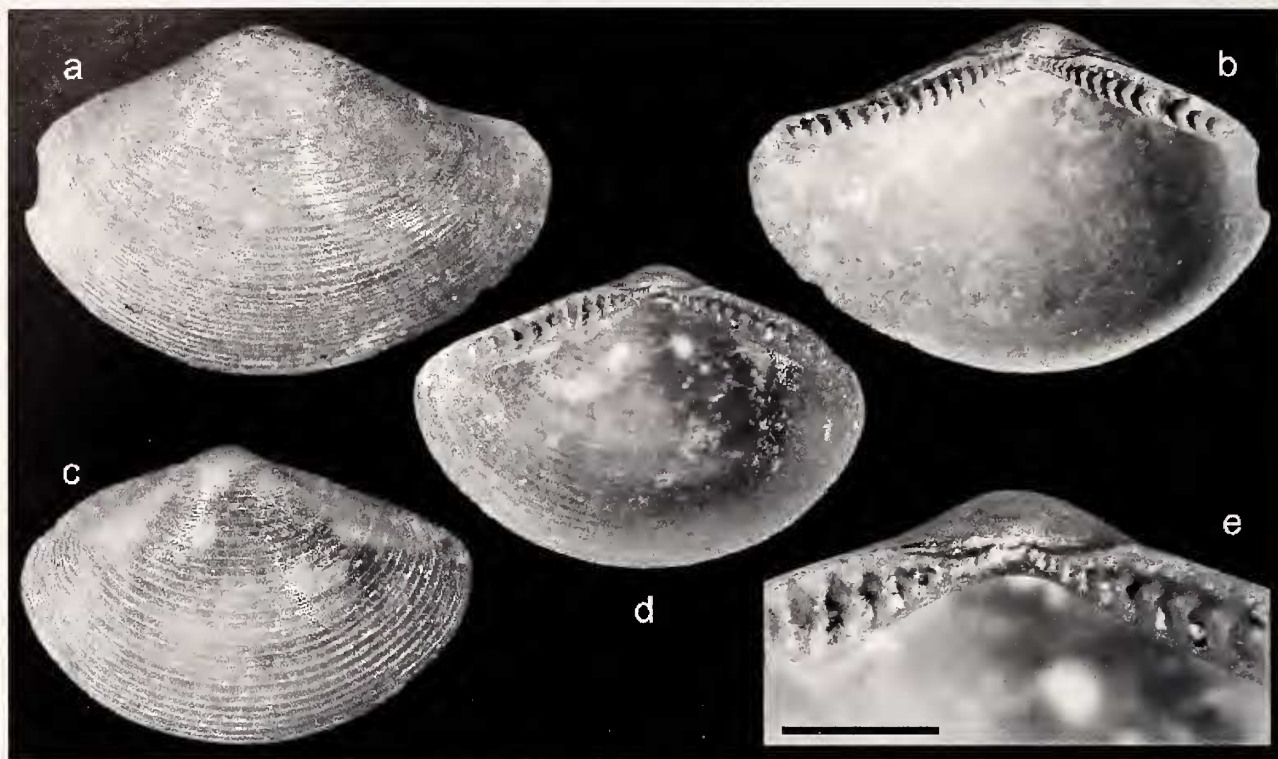


Figure 2. *Neilonella corpulenta* (Dall, 1881), syntypes, Blake Exp., st. 21, Cuba, off Bahia Honda, 525 m, MCZ 007951. a, b. 7.8 mm. c–e. 6.8 mm. Scale bar 1 mm.

difference lies in shell robustness and sculpture strength: the delicate, almost smooth shell of *Austrotindaria* strongly contrasts with the sturdy, sculptured shell of *Neilonella*. No pallial sinus was described for *Austrotindaria*, and examination of the type material failed in detecting a pallial line, sinus and even muscle scars. The species of the family Tindariidae Verrill & Bush, 1897 lack siphons and a pallial sinus (Sanders & Allen, 1977), but their ligament is mainly posterior, widely extending anteriorly and, apparently, with no internal component (Verrill & Bush, 1898; Knudsen, 1970; Sanders & Allen, 1977).

Some Recent and Cenozoic species from New Zealand are assigned to *Austrotindaria*, such as *A. benthicola* Dell, 1956, *A. flemingi* Dell, 1956 (Dell, 1956: pl. 2, figs. 12–15; external views of holotypes are available in the website of the Te Papa Tongarewa Museum, New Zealand) and *A. mawherensis* Maxwell, 1988 (Maxwell, 1988a: pl. 2, figs. 2a, b, d). These species seem to agree with the type species of *Austrotindaria*, except for their weak posterior rostration, which is practically absent in *A. wrighti* ("No indication of rostrum": Fleming, 1948).

Other Cenozoic species from New Zealand are assigned to *Pseudotindaria* Sanders & Allen, 1977 (Maxwell, 1988b, 1992; Beu & Maxwell, 1990). This genus is conchologically similar to *Tindaria* Bellardi,

1875 (family Tindariidae), but differs in possessing siphons (Sanders & Allen, 1977). However, none of the fossil species from New Zealand seems to have the rounded or shortly ovate, poorly inequilateral shell shape of *Pseudotindaria*, as seen in the type species *P. erebus* (Clarke, 1974) (Sanders & Allen, 1977: figs. 29, 31, 39; Warén, 1989: figs. 19a, b). Rather, these species closely match *Pseudoneilonella* in shape, sculpture and ligament characters.

Neilonella and *Austrotindaria* were also applied by Coan et al. (2000) to some protobranchs from Western North America, but the ligament characters were inverted, i.e., opisthodetic in *Neilonella*, amphidetic in *Austrotindaria*. However, none of those species appears to be well allocated in these genera.

Four fossil species from the Mediterranean area, studied in the present work, form a morphologically homogeneous group, markedly similar to *Neilonella* in shell shape and sculpture, but with an opisthodetic ligament. At least two Atlantic living species also belong to this group: *Pseudoneilonella latior* (Jeffreys, 1876) and *P. guineensis* (Thiele, 1931). The shell-ligament system is thought to bear strong characters for limiting related groups within the Protobranchia (e.g., Allen & Hannah, 1986; Warén, 1989; Ockelmann & Warén, 1998) and, as far as is known, there is no gradual transition between the amphidetic condition of

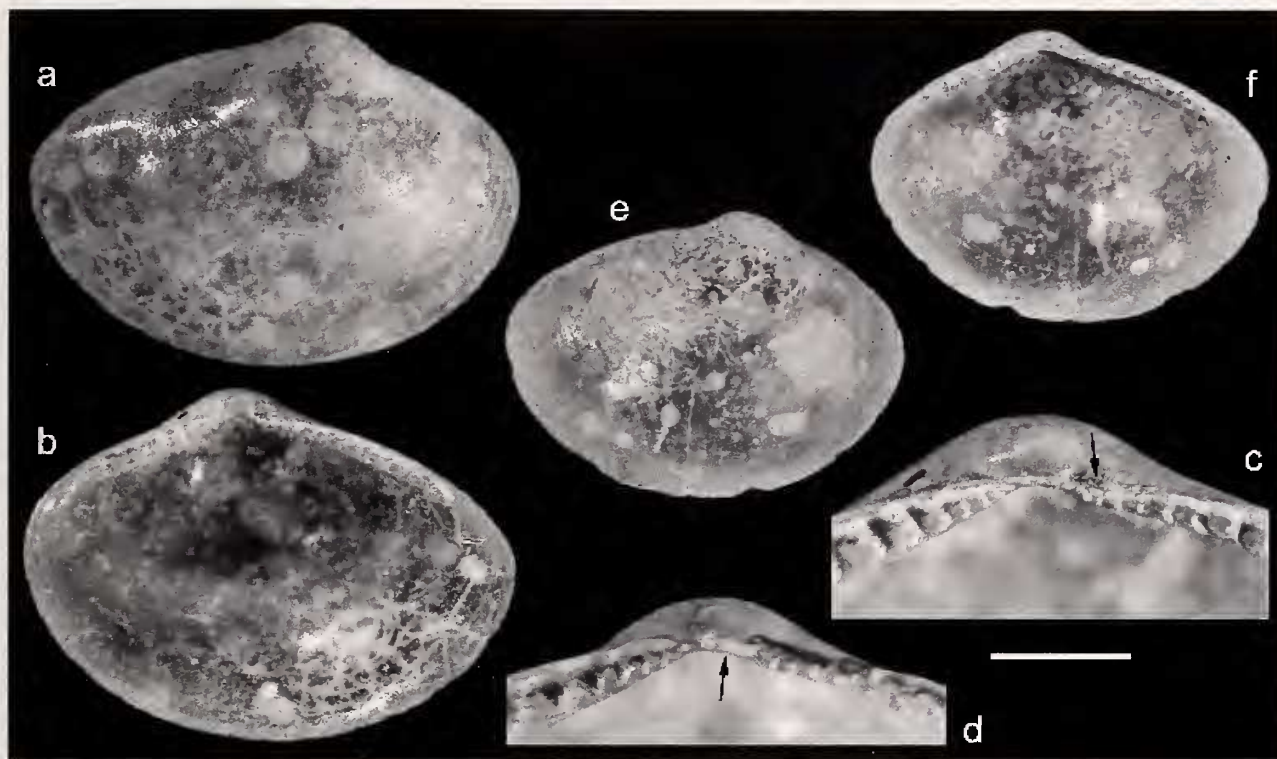


Figure 3. *Austrotindaria wrighti* Fleming, 1948, New Golden Hind Exp., st. 39, Northport, New South Wales, 106 m. a–d. Holotype, 3.6 mm, IGNS, TM109. c,d. standard and oblique views of hinge (note the external posterior ligament in c and the thin, inner ligament pit in d), scale bar 0.5 mm; e, f. Paratype, 2.9 mm, IGNS, TM110. The type material includes a second paratype (left valve) from st. 52, east of Pigeon Island, 40 m (Fleming, 1948: p. 73). It is a different, thin-shelled, subrostrate species with a triangular resilifer, which can be referred to the genus *Yoldiella* Verrill & Bush, 1897. Apparently, this valve was not used in the description of *A. wrighti*.

Neilonella and the opisthodetic one of *Austrotindaria* and *Pseudoneilonella*. For this group of species, a systematic position in the genus *Pseudoneilonella* is then proposed.

Pseudoneilonella pusio (Philippi, 1844)

(Figures 4a–l, 7a, b, g, h, j–m, o)

Nucula pusio Philippi, 1844: 47, pl. 15, fig. 5.

Pseudoneilonella salicensis: Laghi, 1986: 191, pl. 5, figs.

1a, b, 3a, b, 4, 5a, b, 6a, b, 7a–c.

Pseudoneilonella montanaroe Laghi, 1986 (*partim*): 193,

pl. 9, figs. 5a, b, 8a, b (non figs. 4a, b, 6a, b, 7).

Neilonella pusio: Warén, 1989: 252, figs. 16 e, f.

Austrotindaria pusio: Di Geronimo & La Perna, 1997: 414, pl. 9, figs. 1–6, 11.

Types: The type material of *Nucula pusio* (Plio-Pleistocene of Calabria, Southern Italy) is unknown (not present in the Philippi coll. at MZHU: H. Scholz, pers. comm.).

Material examined: Vrica, Pliocene/Pleistocene bound-

ary stratotype, 7 vs. Bianco, Early Pleistocene, 36 vs. Furnari, Early Pleistocene, 74 vs. Fiumefreddo, Early Pleistocene, 132 vs. 3 shs. Archi, Early-Middle Pleistocene, ca 600 vs. 15 shs. Lazzaro, Early-Middle Pleistocene, 126 vs. Catrica, Early-Middle Pleistocene, 69 vs. 2 shs.

Description: Shell small, ovate-trigonal, not very elongate, inequilateral, moderately inflated and sturdy. Umbo small, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly convex to almost straight; junction with posterior margin subangulate. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex. A smooth, obscure keel from umbo to postero-ventral angle, close to dorsal margin. Lunule small, depressed, fairly distinct, es-cutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, ill defined to lost towards umbo and postero-dorsally. Hinge plate robust, somewhat angled, with chevron-shaped teeth in a single series, sometimes divided into two rows by an ill defined edentulous gap or a small pit. Juveniles with an

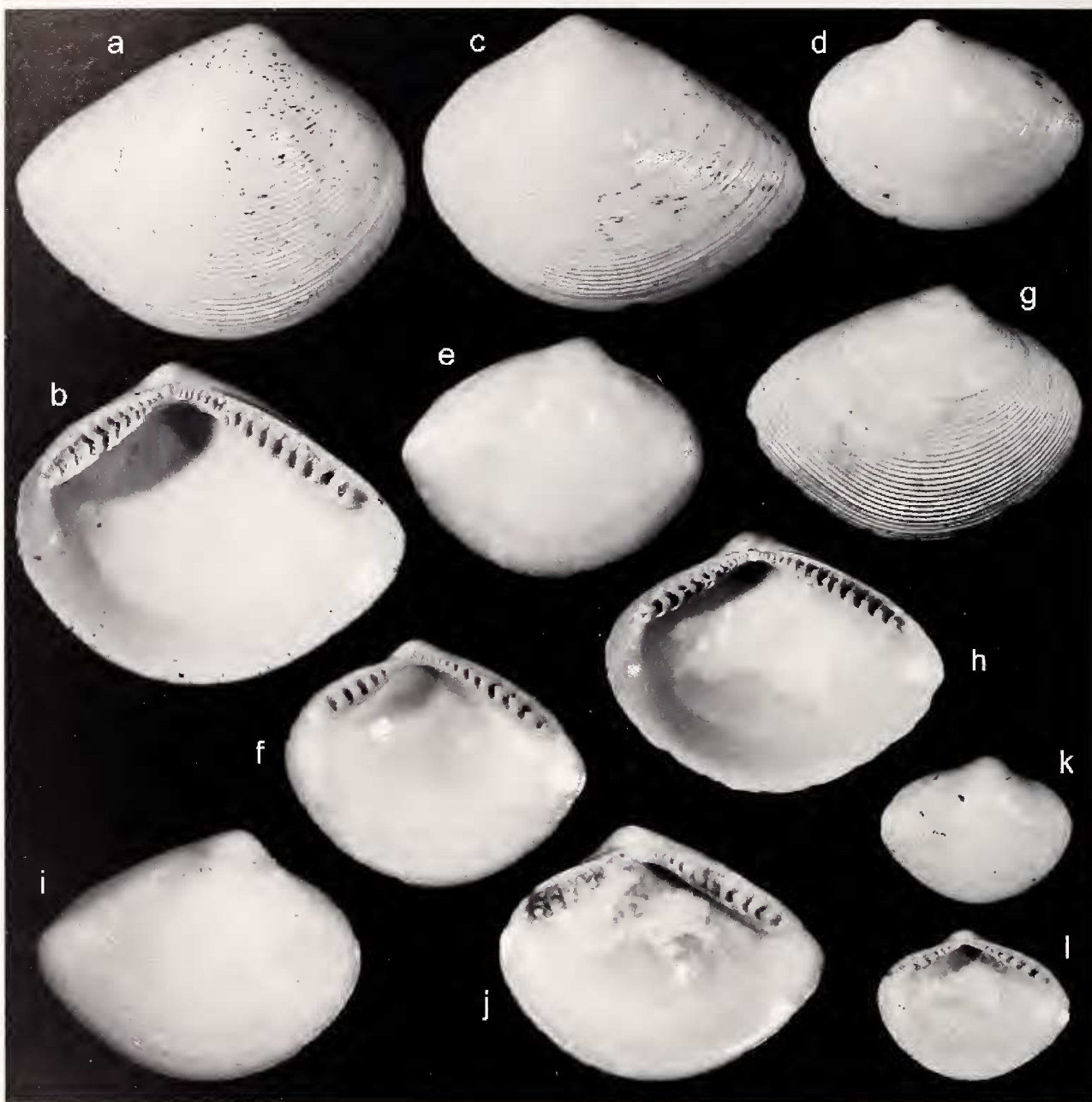


Figure 4. *Pseudoneilonella pusio* (Philippi, 1844). a–f, k, l. Archi, Early-Middle Pleistocene. a, b. 4.5 mm, MZB 29741. c. 4.4 mm, MZB 29741. d. 3.2 mm, MZB 29741. e, f. 3.5 mm, MZB 29741. k, l. 2.3 mm, MZB 29741. g, h. Bianco, Early Pleistocene, 3.9 mm, MZB 29742. i, j. Fiumefreddo, Early Pleistocene, 3.8 mm.

internal, roundish ligament pit beneath beak. Anterior row shorter and stronger than posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, not markedly deep posterior sinus. Prodissoconch ovate, about 215 μ m in maximum diameter. Maximum shell size 6.4 mm (L).

Distribution: It is one of the most common proto-branches in the Early to Middle Pleistocene bathyal assemblages (Di Geronimo & La Perna, 1997; Di Geronimo et al., 1998; La Perna, 2003). It was also present, apparently less commonly, in the earliest Pleistocene (Calabrian) and in the latest Pliocene (Gelasian). The occurrence in the older Pliocene needs

confirmation; some Miocene records reported in the past and modern literature are discussed below.

Remarks: *Nucula pusio* was described as a fossil from Bianco (southern Calabria), where Pliocene and Pleistocene clayey deposits with bathyal associations crop out widely (Di Geronimo & La Perna, 1997). The exact location of the original outcrop is unknown and a possible topotype, from Early Pleistocene beds, is here illustrated (Figures 4g, h; see also Di Geronimo & La Perna, 1997: pl. 9, figs. 1, 3, 4, 6, 11). The expression *fovea ligamenti non conspicua* (= ligament pit not visible), in the original description (Philippi, 1844: 47, pl. 15, fig. 5), does not indicate that the species has a “small resilifer” as misinterpreted by Laghi (1986). On the other hand, *Ledella messanensis* (see above) has a distinct ligament pit.

Pseudoneilonella pusio is well characterised by the strongly convex ventral margin and the attenuation of sculpture posteriorly and postero-dorsally.

Pseudoneilonella montanaroe Laghi, 1986 includes *Pseudoneilonella pusio* (from a Pliocene locality in southeastern Sicily) and *P. latior* (NE Atlantic, Jeffreys coll.), both represented by rather juvenile shells (about 3.0 mm in length). Formally, *Pseudoneilonella montanaroe* (emended as *montanaroe*) should be considered a junior synonym of *P. latior*, since the holotype (Laghi, 1986: pl. 9, figs. 6 a, b) is based on this species.

Pseudoneilonella salicensis (Seguenza, 1877)

(Figures 5a–p, 7c–f, n, p)

Leda (Saturnia) pusio var. *salicensis* Seguenza, 1877a: 96.

Leda (Saturnia) pusio var. *salicensis* Seguenza, 1877b: 18, pl. 4, fig. 20.

Austrotindaria salicensis: Di Geronimo & La Perna, 1997: 416, pl. 9, figs. 7–9.

Leda (Saturnia) pusio var. *salicensis*: Bertolaso & Palazzi, 2000: 32, figs. 124, 125 (type).

Types: Museo di Paleontologia dell'Università di Firenze, Seguenza coll., 4 vs (syntypes).

Material examined: Rometta, Middle Pliocene 30 vs, 4 shs. Rio Gambellaro, Middle Pliocene, 50 vs, 9 shs. Vrica, Pliocene/Pleistocene boundary, 67 vs, 24 shs. Salice, Early-Middle Pleistocene, 3 vs.

Description: Shell small, ovate-trigonal, weakly elongate, inequilateral, markedly inflated and sturdy. Umbo large, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly convex to almost straight; junction with posterior margin subangulate to moderately pointed. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex.

A smooth, obscure keel from umbo to postero-ventral angle, close to dorsal margin. Lunule small, depressed, fairly distinct, escutcheon elongate. Surface with low, fine, closely spaced commarginal ridges, becoming weaker to ill defined towards umbo. Hinge plate notably robust, somewhat angled, with chevron-shaped teeth in a single series, sometimes divided into two rows by an ill defined edentulous gap or pit. Juveniles with an internal, roundish ligament pit beneath beak. Anterior row shorter and stronger than posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, deep posterior sinus. Prodissoconch ovate, about 215 µm in maximum diameter. Maximum shell size about 5.0 mm (L).

Distribution: The known distribution ranges from Middle Pliocene (Piacenzian) to Early Pleistocene. It is uncommon in the Pleistocene deposits.

Remarks: Di Geronimo & La Perna (1997) proposed an identity for *Leda (Saturnia) pusio* var. *salicensis* on topotypic material from Salice (Messina) and the type material reported by Bertolaso & Palazzi (2000: 32, figs. 124, 125) confirmed this identity.

As originally described, *Pseudoneilonella salicensis* is more inflated and sturdily built than *P. pusio*. The ventral margin is less convex, the hinge angle is slightly wider (125°–129° in *P. salicensis*, 120°–123° in *P. pusio*) and the sculpture is more uniform across the shell surface. Puzzlingly, this species was said by Seguenza (1877b) to be more similar to the Atlantic material sent to him by Jeffreys, than to typical *P. pusio*. The Atlantic species is *Pseudoneilonella latior* (Jeffreys, 1876), which is notably less convex and robust, more ovate and elongate (Warén 1989: figs. 16 a–d; Salas, 1996: figs. 52–54). Probably, Seguenza based his opinion mainly on the shell outline, which is somewhat ovate in *P. salicensis* and *P. latior*, rather than roughly squared as in *P. pusio*.

Pseudoneilonella salicensis is more variable than *P. pusio*, particularly in shell elongation and sharpness of the posterior end. It was not possible to separate some markedly “pointed” shells (Figures 5 l–p) from the others with a blunter posterior end. A similar variability was noted by Verrill & Bush (1898: 879) on *Neilonella subovata* Verrill & Bush, 1897 (= *Pseudoneilonella latior*): “Some [specimens] are decidedly more elongated and tapered posteriorly ... others are somewhat shorter and more regularly ovate with the posterior end blunter or more rounded”.

As discussed above, the present species is neither *Neilonella salicensis* of Laghi (1986) (= *Pseudoneilonella pusio*), nor *Neilonella salicensis* of Allen & Sanders (1996) (= *P. latior*).

Robba (1981: 136, pl. 10 figs. 4–7, pl. 11, fig. 1) reported *Saturnia pusio salicensis* from the Early



Figure 5. *Pseudoneilonella salicensis* (Seguenza, 1877). a–c. Rometta, Middle Pliocene: a, b. 4.4 mm, MZB 29743. c. 3.5 mm, MZB 29743. d, e. 3.1 mm. f–i. Rio Gambellaro, Middle Pliocene. f, g. 4.6 mm. h. 3.7 mm, MZB 29744. i. 2.3 mm. j–p. Vrica, Pliocene/Pleistocene boundary stratotype. j, k. 4.8 mm, MZB 29745. l, m. 3.7 mm. n. 2.3 mm, MZB 29745. o. 2.8 mm. p. 3.1 mm, MZB 29745.

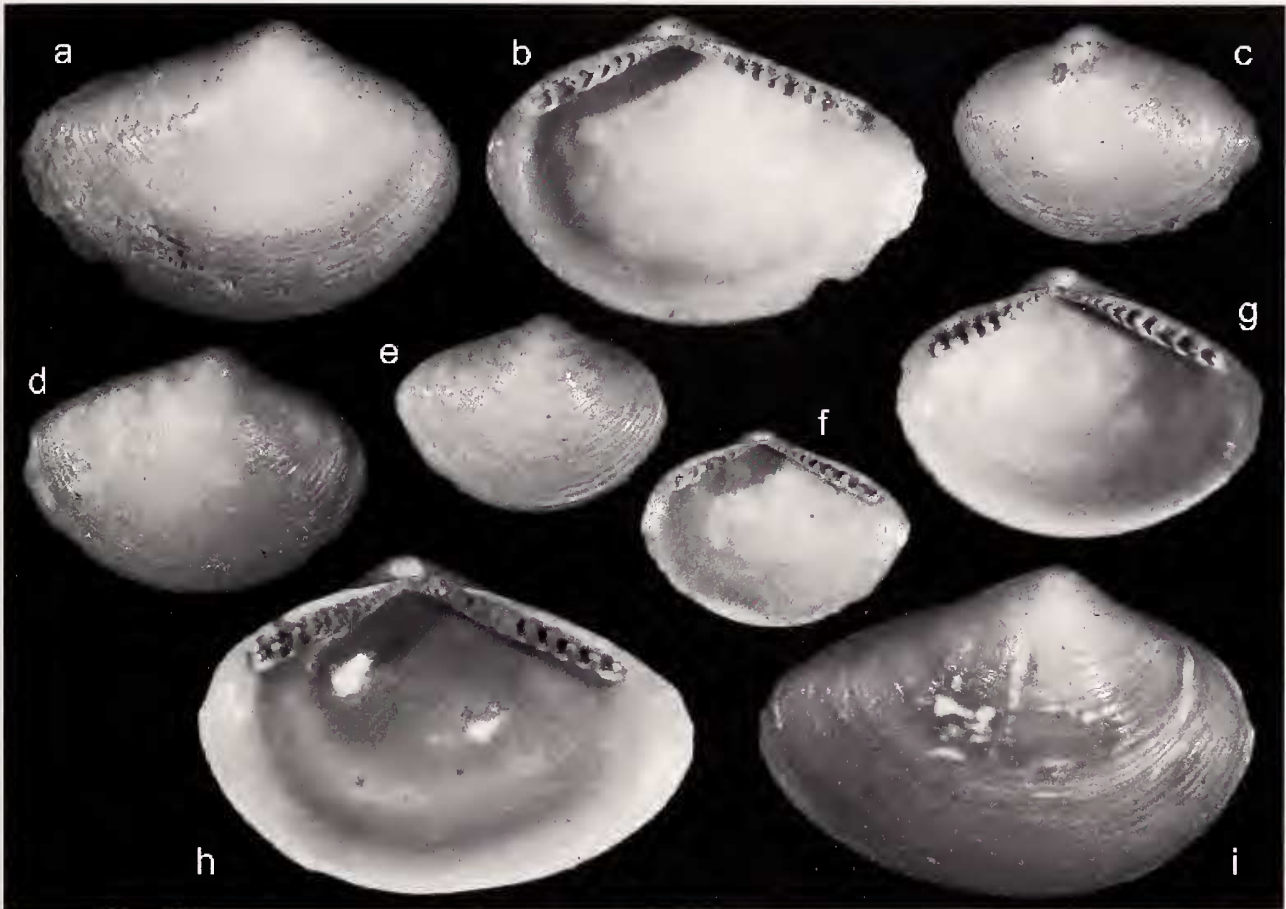


Figure 6. *Pseudoneilonella tenella* La Perna, sp. nov. a–g. Grammichele (Valle Palione), Early Pleistocene: a, b. Holotype, 3.5 mm, MZB 29746. c. Paratype 1, 2.5 mm, MZB 29747. d. Paratype 2, 2.8 mm, MZB 29747. e, f. 2.2 mm. g. 3.0 mm. h, i. Rio Gambellaro, Middle Pliocene, 4.0 mm.

Pliocene of Liguria. Excluding one specimen (pl. 10, figs. 4a, b), which is most probably a species of *Ledella*, the other illustrations actually depict a species of *Pseudoneilonella*, similar in shape to *P. salicensis*, but much smaller (not exceeding 2.5 mm in length) and with a coarser, less dense sculpture. It is probably an undescribed species, here tentatively referred to as *Pseudoneilonella* sp.

Pseudoneilonella tenella La Perna, sp. nov.

(Figures 6a–i, 7i)

Type material: Holotype, MZB 29746 and 2 paratypes, MZB 29747.

Type locality: Grammichele (Valle Palione), southeastern Sicily, Early Pleistocene upper bathyal marls underlying richly fossiliferous coarse sands with *Arctica islandica* (Linné, 1767)

Material examined: Grammichele, Early Pleistocene, 12

vs, 1 sh, including type material. Rio Gambellaro, Middle Pliocene, 2 vs.

Etymology: From the Latin *tenellus* (= diminutive of *tener*, tender, delicate), due to the delicate appearance.

Description: Shell small, ovate, weakly elongate, inequilateral, moderately inflated and thin-walled. Umbo small, leaning out from shell outline, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, straight to barely convex; junction with posterior margin rounded to obscurely angled. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, convex. Lunule small, depressed, fairly distinct, escutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, slightly coarser anteriorly, poorly defined towards umbo. Hinge plate relatively robust, somewhat angled, with chevron-shaped teeth in a single series, or divided into two rows by a small ligament pit. Anterior row shorter than

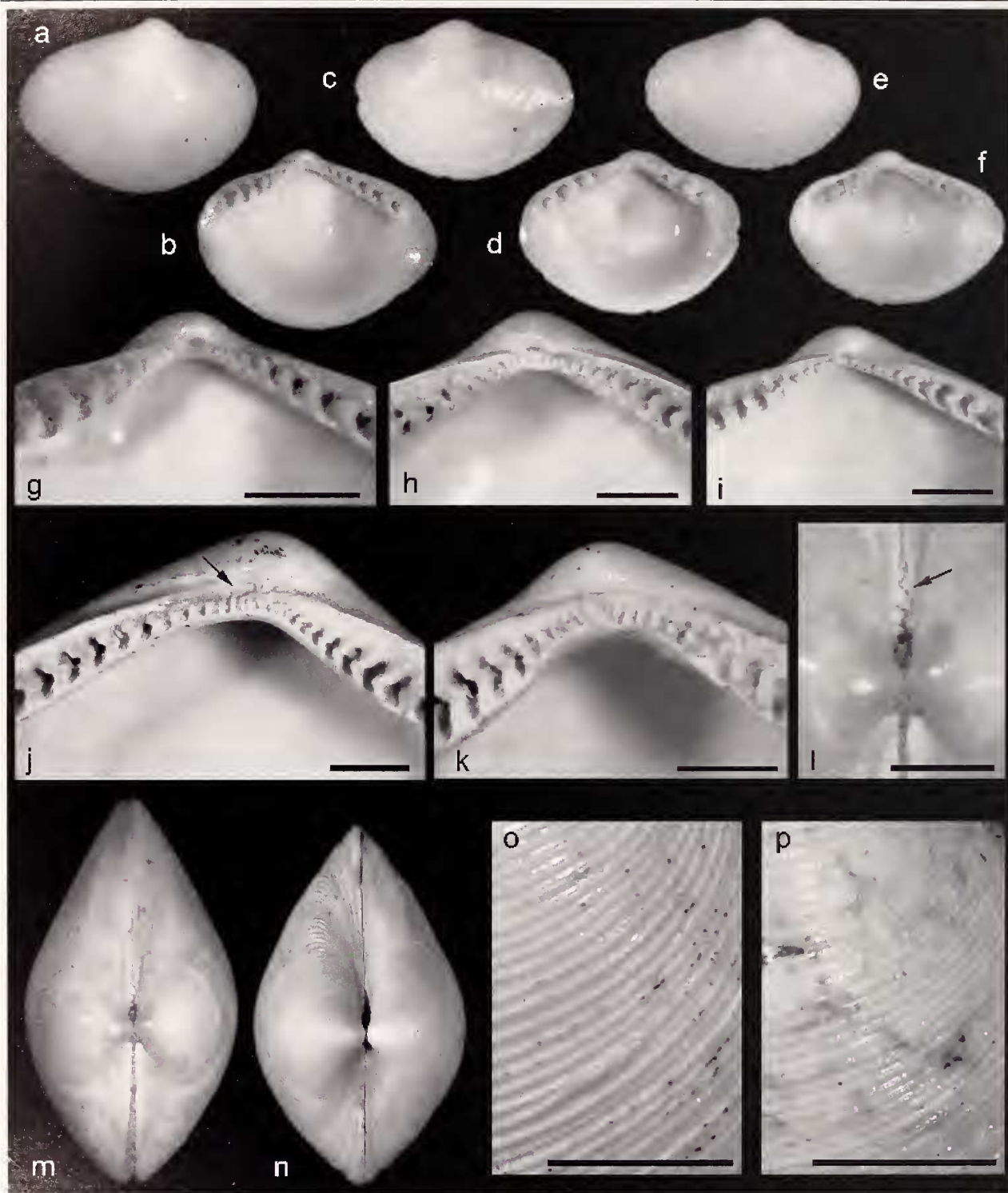


Figure 7. a–f. Juvenile stages. a, b. *Pseudoneilonella pusio*, Archi, 2.3 mm. c–f. *Pseudoneilonella salicensis*. c, d. Rometta, 1.2 mm. e, f. *Vrica*, 1.6 mm. g–l. Details of hinge. g, h. *Pseudoneilonella pusio*. g. Archi, 2.3 mm (same as 7a, b). h. Bianco, 3.9 mm (same as 4g, h). i. *Pseudoneilonella tenella* La Perna, sp. nov., Grammichele (Valle Palione), 3.8 mm (same as 6g). j. *Pseudoneilonella pusio*, Bianco, 4.6 mm (note the well developed external furrow for ligament insertion). k. *Pseudoneilonella pusio*, Archi, 4.5 mm (same as 4a, b). l. *Pseudoneilonella pusio*, Archi, 4.1 mm (note the external posterior ligament furrow through which dentition is seen). m. *Pseudoneilonella pusio*, Archi, 4.1 mm. n. *Pseudoneilonella salicensis*, *Vrica*, 3.9 mm. o, p. Sculpture details, anterior side. o. *Pseudoneilonella pusio*, Archi. p. *Pseudoneilonella salicensis*, *Vrica*. Scale bars 0.5 mm.

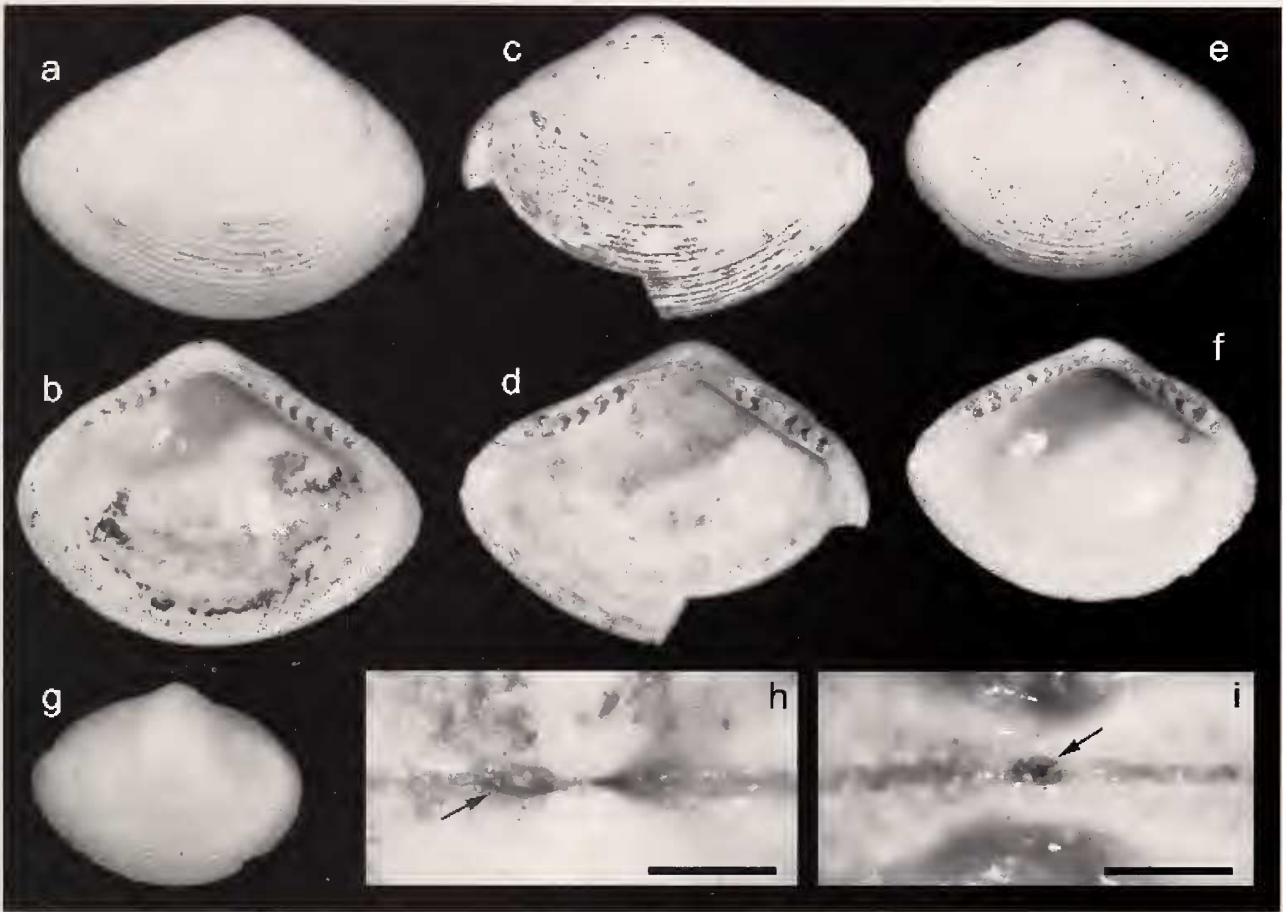


Figure 8. *Pseudoneilonella taurinensis* La Perna, sp. nov. a–i. Monte dei Cappuccini, Turin hills, Langhian, MRSN, Bellardi & Sacco coll., BS 123.04.09/03. a, b. Holotype, 2.7 mm. c, d. Paratype 1, 2.7 mm. e, f. Paratype 2, 2.3 mm. g. Paratype 3, 1.8 mm. h, i. Umbonal fragment of a closed shell, external and internal view (note the external ligament furrow and the internal ligament pit). Scale bars 0.5 mm.

posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, not particularly deep posterior sinus. Prodissoconch ovate, about 200 μ m in maximum diameter. Measurements: holotype 3.5 mm (L), 2.4 mm (H); paratype 1, 2.5 mm (L), 1.8 mm (H); paratype 2, 2.8 mm (L), 2.0 mm (H).

Distribution: Middle Pliocene to Early Pleistocene, but the Pliocene record needs confirmation.

Remarks: *Pseudoneilonella tenella* La Perna, sp. nov., formerly tentatively treated as a shallower ecotype of *Pseudoneilonella pusio* (La Perna, 2003), differs from *P. pusio* and *P. salicensis* by being more delicate, less convex and smaller. The umbo is clearly distinctly above the shell outline. It is somewhat similar to *Pseudoneilonella latior*, from which it differs mainly by being much smaller, less elongate and with a more prominent umbo.

The scarce material from the Middle Pliocene of Romagna differs subtly from the Pleistocene material, by being slightly larger and more inflated, with a better defined posterior rostration and a less dense sculpture. This material is tentatively referred to as *Pseudoneilonella tenella* La Perna, sp. nov. but more material is needed for better understanding its taxonomic status.

Pseudoneilonella taurinensis La Perna, sp. nov.

(Figures 8a–i)

Type material: Holotype and 5 paratypes, MRSN, Bellardi & Sacco coll. (ex Forma coll.), BS 123.04.009/03.

Type locality: Monte Cappuccini, Turin hills, Langhian.

Material examined: The types and 21 vs, 8 shs from the type locality. Sciolze and Pian dei Boschi, Turin hills,

generic Early-Middle Miocene, MRSN, Bellardi & Sacco coll. (ex Rovasenda coll.), BS 123.04.009/02, 7 shs.

Distribution: Middle Miocene (Langhian), Turin hills.

Etymology: After *taurinensis* (= from Turin), Latin.

Description: Shell minute, ovate-trigonal, weakly elongate, inequilateral, moderately inflated and robust. Umbo small, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly concave to almost straight; junction with posterior margin subangulate. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex. Lunule small, depressed, fairly distinct, escutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, evenly distributed from umbo to ventral margin. Hinge plate relatively robust, somewhat angled, with chevron-shaped teeth in two series, separated by a small, slightly elongate ligament pit. Anterior row slightly shorter than posterior. Externally, a narrow, notably short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a rather wide sinus. Prodissoconch ovate, about 170 μ m in maximum diameter. Measurements: holotype 2.7 mm (L), 2.0 mm (H); paratype 1, 2.7 mm (L), 2.0 mm (H); paratype 2, 2.3 mm (L), 1.8 mm (H); paratype 3, 1.8 mm (L), 1.3 mm (H). Maximum shell size about 3.0 mm (L).

Remarks: The finding of neilonellid material in the Bellardi & Sacco coll. was totally unexpected. The record of *Neilonella pusio* by Sacco (1898) from the Late Miocene of Northern Italy is based on a manuscript record by Doderlein of a distinct species belonging to the genus *Ledella* Verrill & Bush, 1897 (Laghi, 1986). The present material was labelled as *Jupiteria broccii* (Bellardi, 1875), a much larger species, of which this material was believed to be a juvenile stage.

Pseudoneilonella taurinensis La Perna, sp. nov. looks almost like a miniature of *P. pusio* in shell shape, inflation and robustness. However, the juvenile stages of the latter (Figures 4k, l) are much smoother, ovate and thin shelled.

The type material is from Langhian deposits (Ferrero Mortara et al., 1982; Pavia, 2000, 2003), whereas the other material is from two localities of generic Early-Middle Miocene age (Ferrero Mortara et al., 1982). The hills rising southwest of Turin consists of a thick succession, Oligo-Miocene in age (Clari et al., 1994). The Early-Middle Miocene succession is characterised by coarse grained beds, due to gravity flows, containing a shallow water fauna and intercalated in marly and silty bathyal deposits (Pavia, 2000, 2003). Most molluscs in the Bellardi & Sacco coll. are from the

allochthonous assemblages, as indicated by the sandy sediment filling the shells. Also the material of *Pseudoneilonella taurinensis* La Perna, sp. nov. is filled with a quartzose-micaceous sand, suggesting an allochthonous origin, i.e., from shallow waters. This contrasts with the Plio-Pleistocene and modern deep water distribution of *Pseudoneilonella*, but other data from the Middle Miocene of Paratethys (see below) suggest a change in the bathymetric distribution of this genus.

Hörnes (1865: 304, pl. 38, figs. 6a–e) reported *Leda pusio* (Philippi) from the Badenian (Middle Miocene) of the Czech Republic (Paratethys). This material was recently illustrated by Schultz (2001: 16, pl. 1, figs. 10, 11) and examined on photographs kindly supplied by O. Schultz. It seems to consist of two species, most probably undescribed and belonging to *Pseudoneilonella*. “*Saturnia pusio*” has also been reported from the Badenian of Austria by Studenka et al. (1998) and Zuschin et al. (2004), from shallow water deposits. The record by Zuschin et al. (2004) was proved to be based on a distinct species, *Leda reussi* Hörnes, 1865 on photographs kindly supplied by M. Zuschin.

CONCLUDING REMARKS

Three, or possibly four bathyal species of *Pseudoneilonella* were present through the Plio-Pleistocene in the Mediterranean area (Figure 9). The increased diversity of neilonellids since the Middle Pliocene seems in agreement with the hypothesis of enhanced psychrospheric conditions and increased diversity of the deep-sea fauna since the Piacenzian, as proposed by La Perna (2003, 2004) but, admittedly, the knowledge of the Early Pliocene bathyal fauna is still rather poor, compared with that of the younger fauna.

In the North Atlantic, *Pseudoneilonella* is represented by *P. latior* (Jeffreys, 1876) ranging from North America, southeastern Greenland and south Iceland to the Ibero-Moroccan Gulf (Warén, 1989; Allen & Sanders, 1996; Salas, 1996). It was also present in the Mediterranean during the Late Glacial, as indicated by old valves in the Tyrrhenian Sea (Di Geronimo & La Perna, 1997: pl. 9, fig. 10). *Pseudoneilonella guineensis* (Thiele, 1931) from West Africa, is similar to *P. pusio*, but notably larger (up to 10 mm in length), more elongate and posteriorly sharper (Knudsen, 1970: fig. 39; pl. 6, figs. 8–10). Two other possible species of *Pseudoneilonella* were described by Allen & Sanders (1996): *Neilonella hampsoni* from the Sierra Leone Basin, and *N. whoii* from the North America Basin.

The origin of the Mediterranean and North Atlantic species of *Pseudoneilonella* is not clear. The occurrence of this genus in Europe (paleo-Mediterranean and Paratethys) ranges back to the Middle Miocene at least. A revision of the Middle Eocene-Pliocene species from New Zealand assigned to *Pseudotindaria* (Maxwell,

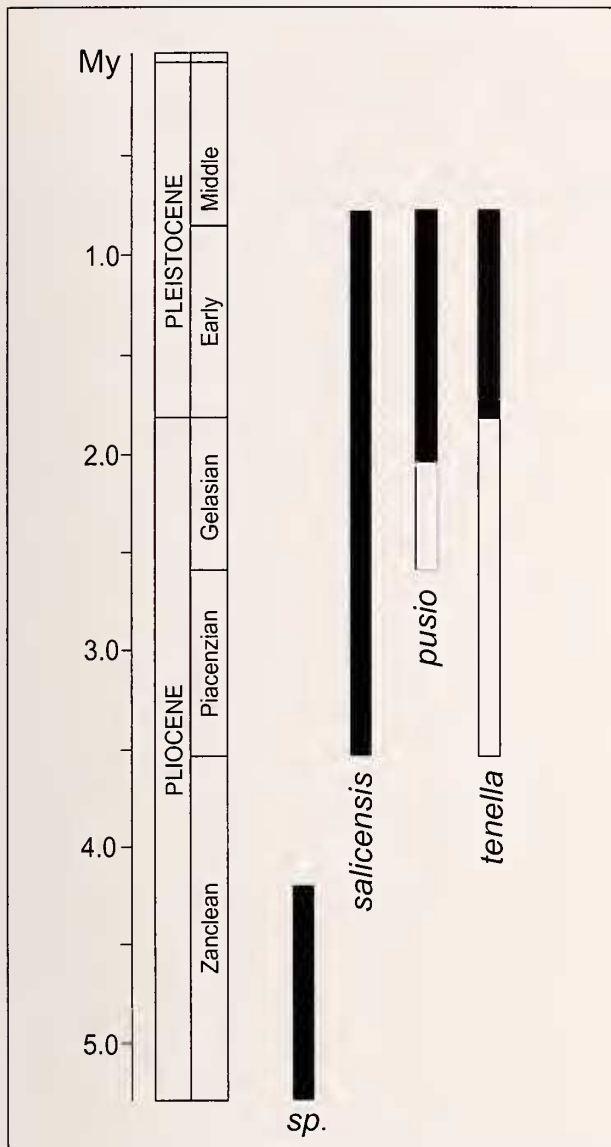


Figure 9. Stratigraphic distribution of the Mediterranean Plio-Pleistocene species of *Pseudoneilonella*. Blank bars indicate dubious data of distribution. Extinctions are arbitrarily positioned at the Early/Middle Pleistocene boundary.

1988b, 1992; Beu & Maxwell, 1990) would be useful to ascertain if they really belong to *Pseudoneilonella*, as suggested in the present work. This may support the hypothesis of a westward diffusion of *Pseudoneilonella*, from the Western Tethys sectors, as proposed for other deep sea European protobranchs (La Perna et al., 2004; La Perna, 2007). Also the study of the Paratethys material could bring useful data to reconstruct the paleogeographic and evolutionary history of *Pseudoneilonella*.

Acknowledgments. Many thanks are due to Adam J. Baldinger (MCZ) for the loan of the type material of *Neilonella corpulenta*, to Alan G. Beu (IGNS) for the loan of the type material of *Austrotindaria wrighti*, to Henning Scholz (MZHU) for useful informations about the Philippi collection, to Cesare Tabanelli (Cotignola, Ravenna) for the loan of material from his own collection, to Martin Zuschin (University of Vienna) and Ortwin Schultz (Naturhistorischen Museum, Wien) for sending photographic documentation and to Anders Warén (Naturhistoriska riksmuseet, Stockholm) for help at various stage and final review of the manuscript. Work supported by Fondi di Ricerca d'Ateneo 2005.

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